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1           **Water bathing alters the speed-accuracy trade-off of**  
2                           **escape flights in European starlings**

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16

17 Birds of most species regularly bathe in water, but the function of this behaviour is  
18 unknown. We tested the hypothesis that water bathing is important in feather  
19 maintenance, and hence should enhance flight performance. We manipulated European  
20 starlings', *Sturnus vulgaris*, access to bathing water in a 2 x 2 design: birds were housed  
21 in aviaries either with or without water baths for a minimum of 3 days (long-term access)  
22 before being caught and placed in individual cages either with or without water baths for  
23 a further 24h (short-term access). We subsequently assessed the speed and accuracy of  
24 escape flights through an obstacle course of vertical strings. Birds that had bathed in the  
25 short term flew more slowly and hit fewer strings than birds that were deprived of bathing  
26 water in the short term, whereas long-term access to bathing water had no significant  
27 effect on flight performance. Thus recent access to bathing water alters flight  
28 performance by altering the trade-off between escape flight speed and accuracy. We  
29 hypothesise that lack of bathing water provision could increase anxiety in captive  
30 starlings because of an increase in their perceived vulnerability to predation. This study  
31 therefore potentially provides an important functional link between the expression of  
32 natural behaviours in captivity and welfare considerations.

33

34 Keywords:

35 animal welfare;

36 dustbathing;

37 European starling;

38 manoeuvrability;

39 passerine;

40 *Sturnus vulgaris*;

41 water bathing.

42

43 Maintenance behaviour has received very little attention from behavioural biologists,  
44 despite forming a significant part of the time budgets of many animals. For example, a  
45 comparative study by Cotgreave & Clayton (1994) found that, across 62 bird species,  
46 individuals spent an average of 9.2% of the day in maintenance behaviours (range 0.3-  
47 25.4%). An important element of avian maintenance behaviour involves bathing in water.  
48 Birds of the majority of species regularly do so, and follow bathing with bouts of  
49 preening and oiling behaviour (Simmons 1964; Slessers 1970). However, in contrast to  
50 dustbathing, which has been the subject of extensive welfare-related research in domestic  
51 fowl (reviewed in Olsson & Keeling 2005), there has been little work on water bathing  
52 since some early descriptive studies.

53         Various hypotheses have been proposed for the benefits of water bathing.  
54 Simmons (1964) suggested that bathing serves to wet the feathers in a controlled fashion  
55 that aids the distribution of preen oil and thus enhances preening. In support of this he  
56 described observations in waders and grebes of birds wetting the bill prior to preening  
57 when no bathing has occurred. Slessers (1970) suggested that bathing serves to squeeze  
58 water through the feathers, ensuring that both skin and feather bases are rinsed. *In vitro*  
59 studies show that water has a direct impact on feather structure (Van Rhijn 1977;  
60 Elowson 1984), suggesting a different mechanism whereby bathing could affect feathers.  
61 Thus, although the precise mechanism is unclear, it seems likely that water bathing has a  
62 function in feather maintenance.

63         Some bird species (e.g. most members of the order galliformes, but also others  
64 including some passerine species) bathe in dust as an alternative or supplementary  
65 substrate to water. Dustbathing is similarly thought to play a role in feather maintenance,

66 specifically in reducing ectoparasite loads and controlling the lipid content of feathers  
67 (Olsson & Keeling 2005). The latter hypothesis has been experimentally confirmed  
68 (Borchelt & Duncan 1974; Van Liere & Bokma 1987), resulting in the suggestion that  
69 there is an optimal lipid load for feathers that balances the beneficial effects of  
70 waterproofing, insulation and improved feather structural integrity against the costs of  
71 feather matting and nourishment for ectoparasites. There is some direct evidence that  
72 dustbathing in Japanese quail, *Coturnix coturnix japonica*, has a function in feather  
73 maintenance (Healy & Thomas 1973). Birds given access to dust showed an  
74 improvement in feather barb alignment immediately after dustbathing in comparison to a  
75 control group denied access to dust.

76 European starlings, *Sturnus vulgaris*, and the majority of passerines bathe  
77 according to the first method described by Slessers (1970, p. 92). That is, they stand in  
78 shallow water and immerse themselves through a set pattern of movements involving  
79 dipping the head and rolling the body to ensure that water is distributed widely. There is  
80 little published information regarding the bathing behaviour (frequency, seasonality, etc.)  
81 of starlings, but they are known anecdotally to be enthusiastic bathers, and  
82 recommendations for husbandry of starlings in the laboratory include provision of water  
83 baths (Hawkins et al. 2001; Asher & Bateson 2008). Our own observations of captive  
84 starlings confirm that they regularly partake in water bathing. Indeed, they commonly do  
85 so when their bathing water has been refreshed, even in the presence of a human  
86 observer. The current experiment was stimulated by our observation that birds that have  
87 just been caught and handled often bathe immediately when released into a cage or aviary  
88 containing fresh bathing water. This suggested to us that bathing, and the following

89 preening routine, might serve a function in repairing feathers disrupted by catching and  
90 handling.

91 A direct test of the hypothesis that bathing facilitates feather maintenance is  
92 difficult. In order to score feather disruption it is necessary to catch and handle a bird,  
93 reversing any benefits of prior bathing. However, since plumage condition is known to  
94 affect flight performance in starlings (Swaddle et al. 1996), we hypothesise that poor  
95 feather maintenance should translate directly into reduced flight performance. We  
96 therefore tested the hypothesis that depriving starlings of the opportunity to water bathe  
97 will impair their escape flight performance, as assessed by their speed and accuracy at  
98 negotiating an aerial obstacle course. Since flight performance is likely to translate into  
99 reduced ability to escape predators or increased tendency to hit obstacles, the fitness  
100 consequences of possible effects of bathing on either speed or accuracy of flight are clear  
101 (Cuthill & Guilford 1990; Lima 1993).

102

103

## 104 **METHODS**

105

### 106 *Subjects*

107 The subjects were 32 (16 male and 16 female) adult European starlings caught from the  
108 wild under licence from Natural England. Prior to the experiment, birds were group-  
109 housed in two indoor aviaries (2.4 x 2.15 x 2.3 m) with wood chippings covering the  
110 floor, dead trees for perching and cover, and shallow trays of water for bathing. The  
111 light:dark cycle was 14:10 h and the temperature was 16-18°C. Throughout the

112 experiment birds were fed a diet of Purina kitten food ad libitum, supplemented with fruit  
113 and mealworms (*Tenebrio* larvae). Our study was approved by the Named Animal Care  
114 Welfare Officer at the Institute of Neuroscience, Newcastle University. Birds were  
115 inspected on a daily basis by technical staff and, following completion of our study,  
116 received a full health inspection by a veterinarian prior to their release to the wild at the  
117 site where they were originally captured.

118

### 119 *Morphological Measures*

120 Prior to their allocation to the experimental aviaries (see below), birds were captured by  
121 hand and several measures were taken. Weight and wing length were measured as  
122 described by Redfern & Clark (2001). It was not possible to weigh the subjects  
123 immediately prior to assessing their flight performance because handling would have  
124 disrupted any plumage condition advantages that bathing might have conferred. We  
125 scored plumage condition by assessing each primary and tail feather as either: complete,  
126 abraded, broken, growing or missing (based on Redfern & Clark 2001).

127 We then allocated subjects to one of three groups on the basis of how many broken  
128 and missing feathers were present: group 1: one or no feathers broken, growing or  
129 missing; group 2: two to four feathers broken, growing or missing; group 3: more than  
130 four feathers broken, growing or missing. Since plumage condition is known to affect  
131 flight performance (Swaddle et al. 1996), equal numbers of birds from each feather  
132 condition group were allocated to the four experimental groups (see below).

133 All birds' bills were lightly trimmed with nail clippers at this time, since bill  
134 morphology affects preening (Clayton et al. 2005). Bill trimming is a recommended

135 standard husbandry technique in starlings, required to prevent overgrowth of one  
136 mandible by the other (Hawkins et al. 2001). For our experiment they were trimmed just  
137 enough to ensure that the mandibles were of equal length.

138

### 139 *Bathing Manipulation*

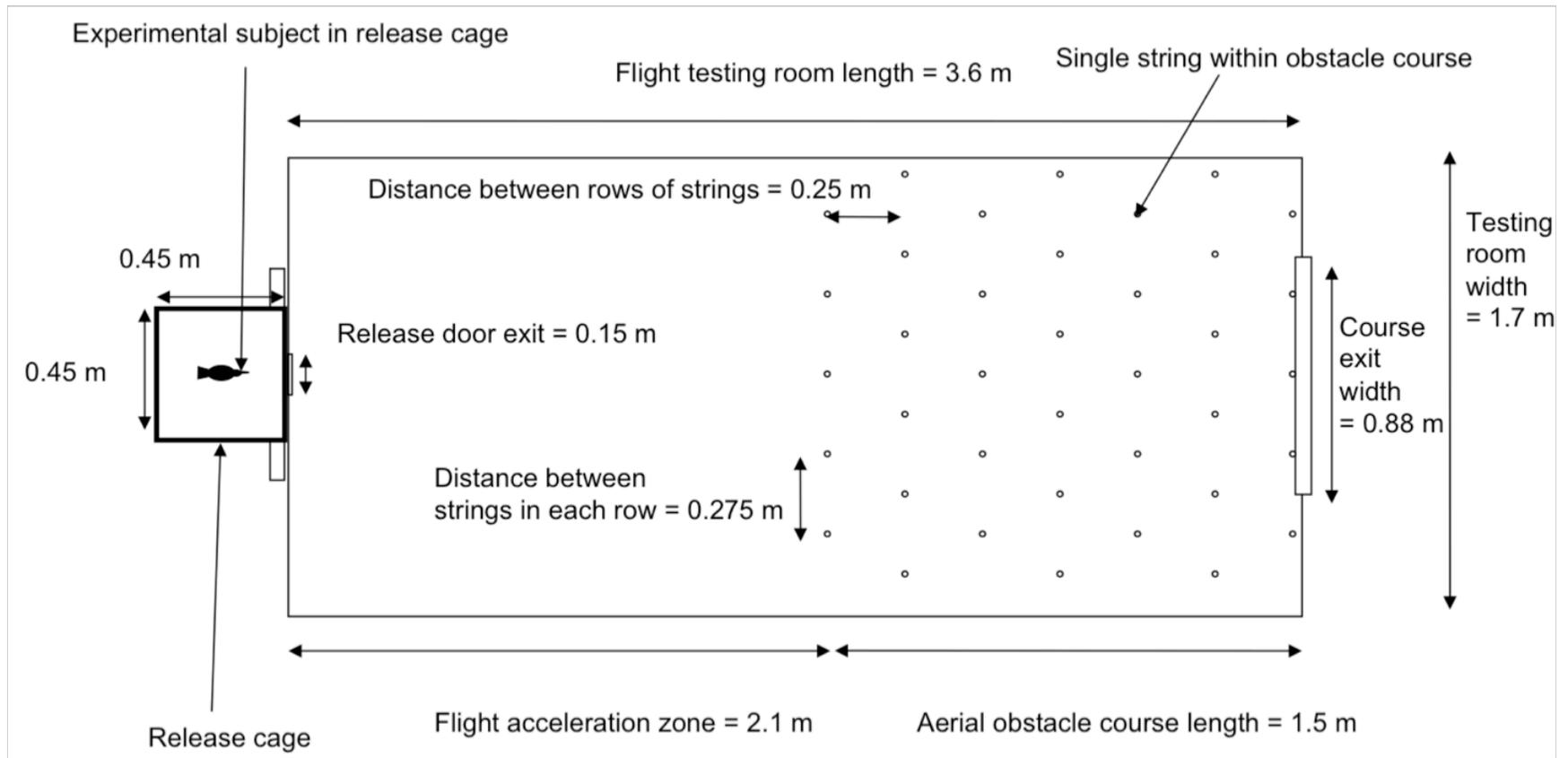
140 We used a 2 x 2 factorial design in which we manipulated both long- and short-term  
141 access to bathing water and assessed the effects of this manipulation on flight  
142 performance. All birds were allocated to one of two long-term groups: either an aviary  
143 with a water bath (500 x 400 x 180 mm deep) filled to a depth of 25 mm (N = 17), or an  
144 aviary with no water bath (N = 15). Birds spent a minimum of 3 days in these aviaries.  
145 The day before flight performance testing, birds were recaptured and transferred to  
146 individual cages (750 x 450 x 440 mm high) located in a separate room. Birds from each  
147 long-term access group were allocated to two short-term groups: birds with short-term  
148 access to bathing water received a water bath (360 x 255 x 60 mm deep) filled to a depth  
149 of 25 mm (N = 16), whereas birds with no short-term access received an empty tray of  
150 the same dimensions (N = 16). Thus each bird fell into one of four possible treatment  
151 groups defined by the combination of long- and short-term access to bathing water it  
152 received. Although each of the four groups contained an equal number of females (N = 4  
153 for all), one male was incorrectly allocated causing unequal numbers of males in long-  
154 term access groups (no access to water: N = 3 males; access to water only in the long-  
155 term: N = 5 males; access to water only in the short-term: N = 4 males; access to water at  
156 all times: N = 4 males).

157           At 0730 hours on the day of flight performance testing, the birds with baths had  
158 their baths cleaned and refilled with fresh water to encourage bathing in the 3 h  
159 immediately prior to testing. The birds without baths had their empty trays cleaned and  
160 returned to match disturbance levels. All 16 birds in the short-term access group bathed in  
161 the 3 h immediately prior to flight performance testing, but were no longer obviously wet  
162 or preening by the time testing began at approximately 1030 hours. Immediately prior to  
163 testing, each bird was induced to walk into a release cage using differential lighting  
164 conditions, and was then transported to the nearby test room. Thus, birds were not  
165 handled between the short-term bathing manipulation and flight performance testing.  
166 Birds were tested in a random order.

167

#### 168 *Testing Flight Performance*

169 We assessed flight performance by releasing birds through an obstacle course of hanging  
170 weighted strings, and recording the number of strings hit and the speed of flight (Witter et  
171 al. 1994; Balmford et al. 2000; Swaddle & Lockwood 2003). The test room (Fig. 1)  
172 consisted of an acceleration area clear of obstacles followed by the strings. The latter  
173 comprised 38 weighted strings hanging from the ceiling, arranged in seven offset rows.  
174 The distance between strings within each row (275 mm) was approximately three-  
175 quarters of the wing-span of an adult starling. The exit from the course opened onto a  
176 well-lit escape room (5.2 x 2.3 x 2.35 m high) containing a dead tree on which birds  
177 could perch. The test room was lit only by light from the escape room to encourage the  
178 birds to fly towards the escape room on release.



**Figure 1.** A plan of the test room (approximately to scale).

179           A release took place as soon as the bird had settled in a location facing the door of  
180 the release cage. We opened the door using a string concurrent with a standardised loud  
181 noise (a digitised recording of a bang) played immediately behind the cage from speakers  
182 at a constant volume and distance to the bird in the cage. The bird's flight was recorded  
183 on a video camera, mounted behind the release cage, running at 30 frames/s, allowing for  
184 later frame-by-frame analysis. Another camera mounted vertically above the exit from  
185 the test room simultaneously monitored the exit from the release cage (using a mirror)  
186 and the exit from the test room.

187           Two measures of flight performance were extracted from the data. We measured  
188 flight accuracy by recording the number of strings each bird hit as it negotiated the  
189 course. Flight time was calculated as the difference between the time of the frame when  
190 the bird passed through the door of the release cage and the time of the frame when its  
191 bill breached the exit to the escape room. Flight time was divided by the length of the test  
192 room (3.6 m) to give flight speed (m/s). All video scoring was conducted blind to the  
193 bathing treatment group of the bird.

194

#### 195 *Statistical Analysis*

196 We used a MANCOVA to examine the effects of bathing treatment group (short term,  
197 long term and their interaction) on our two dependent measures of flight performance  
198 (number of strings hit and speed). To refine our selection of covariates, we excluded  
199 those that were highly correlated with any that had already been selected for inclusion in  
200 the model. Since body weight (g) was significantly correlated with wing length (mm) ( $r_{31}$   
201 = 0.535,  $P = 0.002$ ) it was the only size-related covariate included. We had six measures

202 of feather damage: wing or tail feathers missing, broken or abraded. To minimise this  
203 number, we grouped any covariates that we had *a priori* reason to presume would have a  
204 similar influence. As previous studies have shown that the absence of feathers (as occurs  
205 in moult) can have implications for flight ability (Hedenström 2003), we grouped  
206 together the feathers missing and feathers broken variables. However, we chose to group  
207 only those measures belonging to the same feather group (wing or tail) since correlations  
208 between different measures from the same feather group (wing or tail) were higher than  
209 for the same measures from different feather groups. This resulted in four feather  
210 measures: wing feathers broken or missing, tail feathers broken or missing, wing feathers  
211 abraded and tail feathers abraded. Of these, the number of tail feathers broken or missing  
212 was marginally nonsignificantly correlated with weight ( $\tau = 0.263$ ,  $P = 0.076$ ; all other  
213 feather variables:  $P > 0.48$ ); hence only the remaining three feather variables were  
214 included with weight as covariates. The interactions between each covariate and separate  
215 experimental factor were also initially included in the model. In line with accepted  
216 practice we excluded covariates (and their accompanying interactions) in a stepwise  
217 manner, removing the least significant term from the model in each step. The covariates  
218 were only removed on condition that the interactions with the experimental treatments  
219 were also nonsignificant (Engqvist 2005). The number of strings hit was square-root  
220 transformed prior to analysis. All assumptions of the performed tests were checked and  
221 held true. Estimates of effect size are given in the form of partial Eta squared ( $\eta_p^2$ ) which  
222 represents the proportion of the total variance (effect + error) that is attributable to the  
223 effect. The weight for one of the subjects was inadvertently not recorded and therefore  
224 any analyses conducted where weight was included as a covariate excluded the data from

225 this subject. Statistical analysis was conducted using SPSS version 16 (SPSS Inc.,  
226 Chicago, IL, U.S.A.).

227

## 228 **RESULTS**

229 Our dependent variables were moderately negatively correlated ( $r_{32} = -0.346$ ,  $P = 0.052$ ),  
230 hence our decision to undertake a multivariate analysis of variance was justified. After  
231 we excluded all nonsignificant covariates and interactions, the resulting model included  
232 weight as the sole covariate because of the significance of the weight\*short-term bathing  
233 manipulation interaction (short-term access to bathing water:  $V = 0.26$ ,  $F_{2,24} = 4.189$ ,  $P =$   
234  $0.028$ ,  $\eta_p^2 = 0.26$ ; long-term access to bathing water:  $V = 0.01$ ,  $F_{2,24} = 0.128$ ,  $P = 0.881$ ,  
235  $\eta_p^2 = 0.01$ ; interaction between short-term and long-term access to bathing water:  $V =$   
236  $0.07$ ,  $F_{2,24} = 0.927$ ,  $P = 0.410$ ,  $\eta_p^2 = 0.07$ ; weight:  $V = 0.12$ ,  $F_{2,24} = 1.633$ ,  $P = 0.216$ ,  $\eta_p^2$   
237  $= 0.12$ ; interaction between weight and short-term bathing manipulation:  $V = 0.24$ ,  $F_{2,24}$   
238  $= 3.730$ ,  $P = 0.039$ ,  $\eta_p^2 = 0.24$ ; all test statistics for the omnibus test produced identical  
239 outputs, hence only that for Pillai's trace is given here).

240 For two reasons we decided to refine our analysis such that the covariate  
241 interaction could be negated. First, examination of the regression slopes revealed that the  
242 interaction occurred primarily because of the differential effect of weight on the speed of  
243 the subjects in each experimental group. Speed increased with weight for birds that had  
244 bathed in the short-term, but speed decreased with weight for birds that had not bathed.  
245 This interaction was unexpected and was probably an artefact given the lack of a  
246 biologically realistic post hoc explanation for the interaction and the multiple covariate  
247 interaction terms included in the full model. Second, we were primarily interested in the

248 effect of treatment manipulations in this study. Hence, we used the Wilcoxon (Johnson-  
249 Neyman) procedure to control for the heterogeneity in regression slopes (Wilcox 1987), a  
250 test that establishes the limits of the covariate for which the treatment groups differ  
251 (Quinn & Keough 2002). The procedure revealed that between weights of 68.3 and 77.4 g  
252 there was no significant difference in the speed of subjects between the two groups. We  
253 excluded any subjects from the analysis that fell outside of this range (leaving a sample  
254 size of N=20), then repeated the MANCOVA as per above. Both weight and the  
255 weight\*short term bathing manipulation interaction had nonsignificant effects in this new  
256 model and hence were excluded to leave a minimal model that included only the  
257 treatment factors. It showed that short-term access to bathing water was still the only  
258 manipulation with a significant effect on flight speed and the number of strings hit (short-  
259 term access to bathing water:  $V = 0.41$ ,  $F_{2,15} = 5.170$ ,  $P = 0.020$   $\eta_p^2 = 0.41$ ; long-term  
260 access to bathing water:  $V = 0.25$ ,  $F_{2,15} = 2.449$ ,  $P = 0.120$ ,  $\eta_p^2 = 0.25$ ; interaction  
261 between short-term and long-term access to bathing water:  $V = 0.24$ ,  $F_{2,15} = 2.374$ ,  $P =$   
262  $0.127$ ,  $\eta_p^2 = 0.24$ ).

263         Having demonstrated robustly that there was an effect of the short-term bathing  
264 water manipulation, we subsequently included all subjects and conducted follow-up  
265 ANOVAs on each dependent variable. These showed that there was no significant effect  
266 of the bathing manipulations on either flight speed (short-term access to bathing water:  
267  $F_{1,28} = 2.13$ ,  $P = 0.155$ ,  $\eta_p^2 = 0.07$ ; long-term access to bathing water:  $F_{1,28} = 0.32$ ,  $P =$   
268  $0.575$ ,  $\eta_p^2 = 0.01$ ; interaction between short-term and long-term access to bathing water:  
269  $F_{1,28} = 0.27$ ,  $P = 0.606$ ,  $\eta_p^2 = 0.01$ ) or number of strings hit (short-term access to bathing  
270 water:  $F_{1,28} = 1.98$ ,  $P = 0.171$ ,  $\eta_p^2 = 0.07$ ; long-term access to bathing water:  $F_{1,28} = 0.59$ ,

271  $P = 0.449$ ,  $\eta_p^2 = 0.02$ ; interaction between short-term and long-term access to bathing  
272 water:  $F_{1,28} = 1.31$ ,  $P = 0.262$ ,  $\eta_p^2 = 0.05$ ) when considered individually (see Figs 2 and  
273 3: data from all subjects are plotted). This suggests that the effect of bathing depended on  
274 the interaction of our two dependent variables.

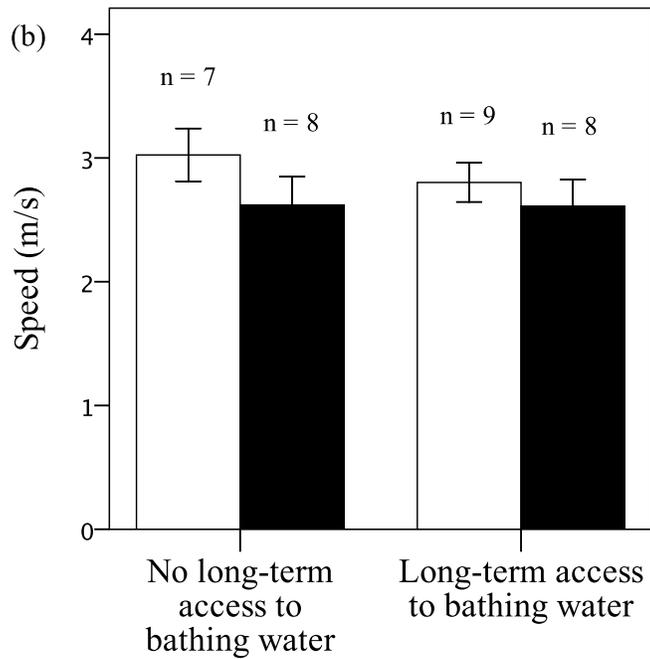
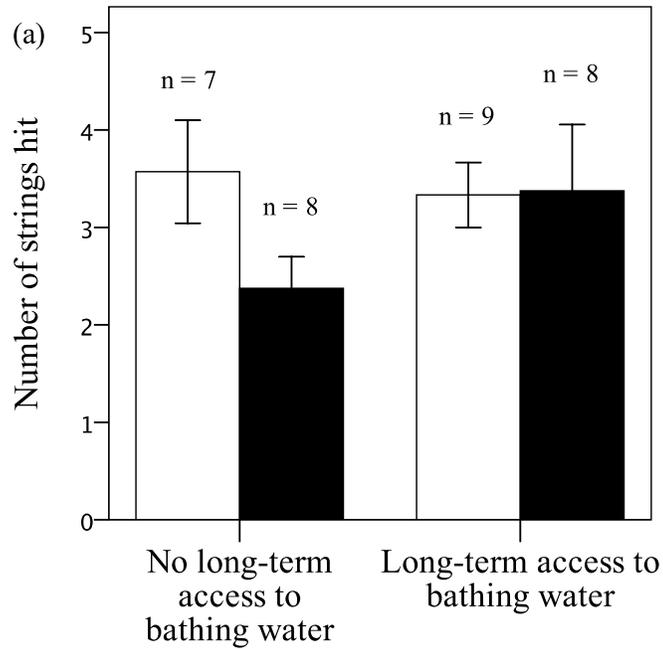
275 To explore this possibility we undertook a discriminant function analysis to  
276 establish how speed or the number of strings hit contributed to the ability to distinguish  
277 subjects in the two short-term bathing experimental groups. The analysis revealed a  
278 single discriminant function with a canonical  $R^2 = 0.19$ . This function significantly  
279 differentiated between birds that had short-term access to bathing water or not ( $\Lambda = 0.81$ ,  
280  $\chi^2_2 = 6.12$ ,  $P = 0.047$ ). The correlation between flight performance measures and the  
281 discriminant function revealed that both measures loaded highly and positively on to this  
282 function (speed:  $r = 0.947$ ; number of strings hit:  $r = 0.936$ ).

283

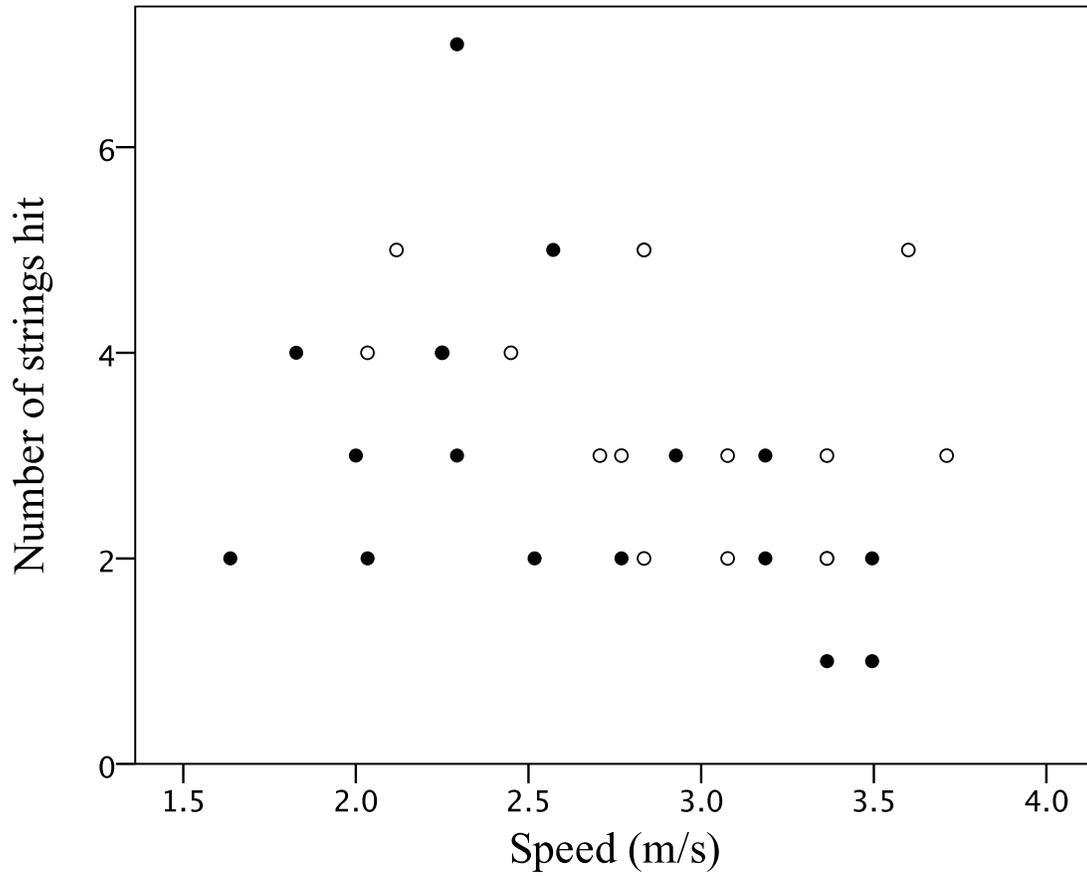
## 284 **DISCUSSION**

### 285 *Effects of Short and Long-term Access to Bathing Water*

286 Our results show that bathing in water in the 3 h prior to a flight test had a significant  
287 impact on flight performance in starlings that had previously had their plumage disrupted  
288 by catching and handling. Birds that had bathed in the short term tended to hit fewer  
289 strings and fly more slowly through the obstacle course. Although this trend was not  
290 statistically significant when each measure was examined individually, our results  
291 suggest that the effect of short-term bathing is manifested in the trade-off between the  
292 speed of escape and the need to avoid collisions. Indeed, the discriminant function  
293 analysis shows that both speed and the number of collisions load highly on to the



**Figure 2.** (a) Mean number of strings the subjects hit during flight and (b) mean speed of subjects through the obstacle course when they had short-term and long-term access to water baths. White bars represent subjects with no access to bathing water in the short-term, black bars represent subjects with access to bathing water in the short term. Error bars represent 1 SE.



**Figure 3.** The relationship between speed through the aerial obstacle course and the number of strings hit. Filled circles represent the data from birds that had short-term access to bathing water. Open circles represent the data from birds that had no short-term access to bathing water.

294 discriminant function that enables differentiation of the two short-term bathing  
295 experimental groups. Additionally, this discriminant function had a canonical  $R^2$  of 0.19,  
296 suggesting that the short-term bathing manipulation caused at least a medium effect size  
297 (Cohen 1992).

298

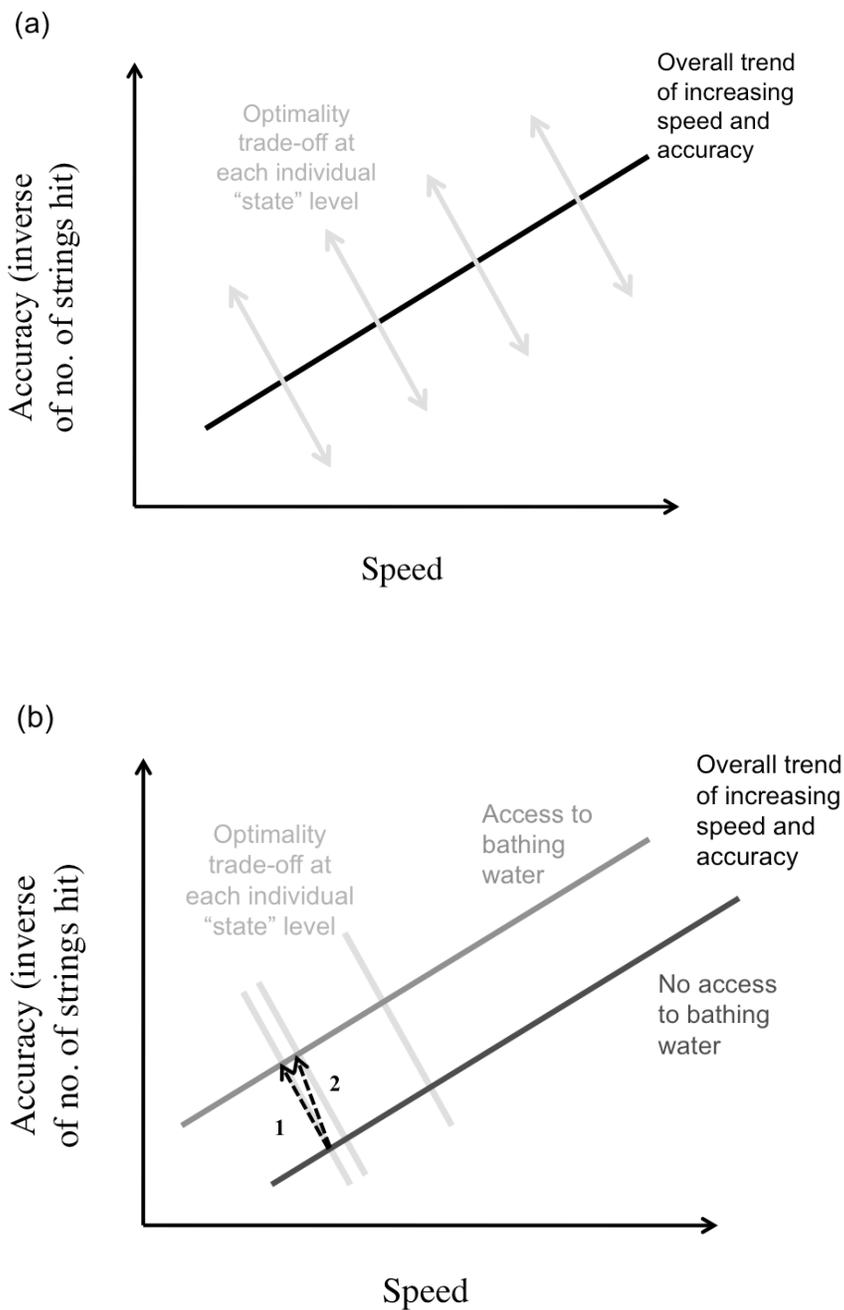
### 299 *Relationship between Speed and Accuracy*

300 Our results show that there was a (marginally nonsignificant) negative correlation  
301 between flight speed and number of strings hit (i.e. there was a positive relationship  
302 between speed and accuracy: see Fig. 3). However, the experimental manipulation  
303 (providing bathing water immediately prior to the flight trials) decreased both flight  
304 speed and the number of strings hit in equal measure (as indicated by the discriminant  
305 function analysis). It therefore increased accuracy but seemingly at the expense of speed.  
306 Below we discuss the implications of this finding within the context of other  
307 experimental results.

308         In agreement with our findings, previous comparable experiments have generally  
309 found that subjects that fly faster through an obstacle course have better accuracy in  
310 avoiding strings (but see Evans et al. 1994 for a partially contradictory finding). Swaddle  
311 & Witter (1998) found that there was no difference in flight speed in starlings with  
312 varying wing asymmetry, but that more symmetrical birds hit fewer strings and tended to  
313 be faster. Witter et al. (1994) found that manipulations of mass had no significant effect  
314 on the time taken to complete an obstacle course, but that weighted birds hit more  
315 obstacles. When a natural manipulation of mass was used (food deprivation) there was a  
316 trend for lighter birds to be faster and hit fewer strings. Similarly, an experiment with

317 house martins, *Delichon urbica*, found that birds with distal parts of the outer tail feathers  
318 trimmed flew both faster and more accurately through an obstacle course (Matyjasiak et  
319 al. 2004). Finally, Balmford et al. (2000) showed that artificially shortening the tail length  
320 in golden-headed cisticolas, *Cisticola exilis*. resulted in decreased speed and more strings  
321 hit, while increasing the tail length resulted in increased speed and accuracy.

322 We propose that *within* individuals there is a trade-off between flight speed and  
323 flight accuracy. However, this trade-off is not apparent *between* individuals because  
324 higher intrinsic flight performance ability is reflected in both higher speeds and improved  
325 accuracy (in much the same way that people with larger houses also tend to own more  
326 expensive cars). This is represented conceptually in Fig. 4a, which shows a speed-  
327 accuracy trade-off within each individual (grey lines), but an overall positive correlation  
328 of speed and accuracy between individuals (black line). The parallel light grey lines in  
329 Fig. 4b demonstrate the potential effect of our experimental manipulation, namely an  
330 average decrease in speed and increase in accuracy. Figure 4b also illustrates the two  
331 possibilities for how the manipulation effected this change: either by altering the  
332 perceived escape flight payoffs for the birds causing them to consider flight speed of less  
333 importance than the reduction in collision risk (parallel dashed arrow in Fig. 4b); or by  
334 causing some mechanical change in flight performance, altering the optimality trade-off  
335 that each individual is able to make (oblique dashed arrow in Fig. 4b). These are not  
336 mutually exclusive hypotheses; indeed it is hard to conceive of how a change in  
337 perceived payoffs could occur without a proximate mechanical means (i.e. a change in  
338 flight performance).



**Figure 4.** (a) A conceptual representation of the relationship between speed and accuracy. (b) A conceptual representation of the experimental manipulation effect. The dark grey line represents subjects that had no access to bathing water, the medium grey line represents subjects that did have access. The dashed black lines represent the proposed experimental effect: the parallel line (labelled 1) represents a change in the optimum of the same speed-accuracy trade-off; the oblique line (labelled 2) represents a change in mechanical flight performance causing a change in the achievable trade-off.

339           A number of proximate functions for bathing have been proposed that might alter  
340 flight performance: realignment of disrupted feather barbules (Healy & Thomas 1973);  
341 aiding the distribution of preen oil (Simmons 1964); enhancing feather flexibility/other  
342 mechanical effects (Van Rhijn 1977); cleansing and removal of dirt (Slessers 1970; Van  
343 Rhijn 1977); and thermoregulation (Thomas & Robin 1977; Oswald et al. 2008). The  
344 current data set unfortunately provides no means of distinguishing between these  
345 competing hypotheses. On the basis of our anecdotal evidence on the increased eagerness  
346 to bathe in birds that had been handled, we favour the explanation of realignment of  
347 feather barbules. However, we must leave the question of mechanism for future  
348 investigation.

349

#### 350 *Welfare Considerations in Captive Passerines*

351 As a possible explanation for our results we suggest that the birds that had bathed in the  
352 short term considered the speed of escape less salient than the need to avoid collisions.  
353 This could be explicable if bathing had reduced perceived risk through a mechanical  
354 improvement in flight performance. Flight manoeuvrability is considered to be an  
355 important factor in birds' ability to escape from predators (Lima 1993; Witter et al.  
356 1994), and reduced ability to deal with predation is reflected in an increased sensitivity to  
357 predation cues and increased aversion to risk (Stankowich & Blumstein 2005). Since  
358 anxiety is the emotional process that deals directly with awareness and interpretation of  
359 threatening stimuli (Lang et al. 2000), an increase in perceived risk of threats is likely to  
360 increase anxiety levels (Loewenstein et al. 2001). In support of our argument, we have  
361 evidence that starlings given access to bathing water subsequently show reduced

362 sensitivity to cues of predation risk (conspecific alarm calls) (Brilot & Bateson, 2012).  
363 Additionally, captive starlings deprived of environmental enrichments, including water  
364 baths, display evidence of a more negative affective state (Bateson & Matheson 2007;  
365 Matheson et al. 2008). Similarly, reduced dustbathing results in increased fear and stress  
366 levels in junglefowl, *Gallus gallus spadiceus*, (Vestergaard et al. 1997) and domestic  
367 chickens, *Gallus gallus domesticus*, (Campo and Muñoz 2001). Selective breeding for  
368 low and high dustbathing lines in Japanese quail have also shown an inverse correlation  
369 between dustbathing and susceptibility to fear (Gerken et al. 1988). We suggest that  
370 anxiety caused by lack of water bathing or dustbathing might act as a mechanism for  
371 increasing risk aversion to avoid potential threats that could not be dealt with in an  
372 optimal fashion because of poor plumage condition. However, we accept that our data  
373 provide only circumstantial evidence to support our discussion of the relationship  
374 between bathing and anxiety.

375         In conclusion, we have shown that bathing alters the trade-off between escape  
376 flight speed and accuracy in starlings, providing the first experimental demonstration of a  
377 potential adaptive value of water bathing in birds. However, the proximate mechanism  
378 for the effect of bathing (mechanical or perceptual) is unresolved. We hypothesise that  
379 depriving birds of opportunities to bathe could result in increased anxiety because of a  
380 compromised ability to escape from predators.

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382

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